SEEDCROP CHARACTERISTICS AND MINIMUM REPRODUCTIVE SIZE OF ORGAN PIPE CACTUS (*STENOCEREUS THURBERI*) IN SOUTHERN ARIZONA

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ABSTRACT

Seedcrop characteristics and the relationship of reproductive activity to size of organ pipe cactus (*Stenocereus thurberi*) were examined in Organ Pipe Cactus National Monument, Arizona. A sample of 19 fruits collected had a mean diameter of 52.9 mm and a mean seed content of 1969 seeds/fruit. Laboratory germination percentage at 20–25°C and a 12 hr photoperiod was 88%. Height measurements and fruit presence/absence observations made at two locations in the Monument indicate that most *S. thurberi* individuals begin to reproduce when they are 2–2.5 m in height. Plants typically have 4–10 arms by the onset of reproductive maturity. Large individuals of *S. thurberi* may produce more than 50 fruits in a season. These results indicate that the reproductive potential of mature individuals of this species is high.

The giant cactus forests of the Southwest have captured the interest of botanists and travelers to that region for over a century. Although three of the columnar cactus species found in the Sonoran Desert occur naturally in the United States, the vast majority of scientific studies on columnar cactus conducted in this country (e.g., Shreve 1910, Niering et al. 1963, Steenbergh and Lowe 1969, 1977, 1983) have focused on saguaro [*Carnegiea gigantea* (Engelm.) Britt. & Rose], the most widespread and conspicuous of the columnar cacti in the United States. In favorable habitats, organ pipe cactus [*Stenocereus thurberi* (Engelm.) Buxb.] (Fig. 1) also is prominent, but its range within the United States is restricted to several populations in southern Arizona (Hastings et al. 1972). It has received much less attention from scholars than *C. gigantea*; consequently, we know less about the basic ecology and population dynamics of *S. thurberi* than of *C. gigantea*. Recent studies have begun to identify ecological characteristics (Nobel 1980, Smith et al. 1984) and site preferences (Yeaton and Cody 1979) of *S. thurberi* in the northern part of its range, but McDonough's (1964) study of factors affecting seed germination is the only work published on the reproductive characteristics of this species.

The purpose of this study was to determine the size at which individuals become reproductively active and the fruit size and seed production and germinability for populations of *S. thurberi* in southern Arizona.

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FIG. 1. Fruiting individual of *Stenocereus thurberi* in Organ Pipe Cactus National Monument.

METHODS

Study area. The study was conducted in Organ Pipe Cactus National Monument (OPCNM), which supports one of the most extensive populations of *S. thurberi* in the United States. Data were collected in late June and early July 1976, approximately midway

through the flowering and fruiting season for reproductively active plants.

Mean annual precipitation at the Monument headquarters is 233 mm (Weather Bureau 1951–1974, NOAA 1975–1980), although data from a network of backcountry raingauges indicate that rainfall is generally higher in the Ajo Mountains along the eastern boundary of the Monument because of orographic uplift (Table 1). For the 17 yr period from 1962–1983 (exclusive of 1967 and 1973–1976 when backcountry records were incomplete), annual rainfall at a remote station in the Ajo Mountains exceeded rainfall at the official weather station in the Monument by a mean value of 101 mm (s.d. = 148 mm, range = −45 to 418 mm). Precipitation is distributed bimodally throughout the year, with the primary rainfall maximum coinciding with the time of fruit maturation during summer and the secondary maximum occurring during winter. Annual precipitation for the year prior to the study (1975) was well below the mean, and the summer of that year was the driest of the last 35 yr (1950–1984; Table 1).

Nocturnal freezes occur occasionally in the Monument ($\bar{X}$ = 19 freezes/year; Table 1), but no subfreezing daily maximum has been recorded at the Monument headquarters in its 42 yr history as a weather station. The winter preceding the study (1975–1976) had a typical number of freezes, with −5°C as the lowest temperature recorded that winter.

Sample sites. To analyze the relationship between size and reproductive activity, data were collected from two sites within OPCNM that had similar slope characteristics. Both were on south–southwest-facing rocky hillsides with slope angles from 15–20° and approximately 25–50 m above the the adjacent valley floor. Both valleys sloped gently southward as part of the Sonoyta River drainage network. Soils in both sites were shallow gravelly loams. The Twin Peaks site (31°57′N, 112°49′W) was located north of the Monument campground (within 2 km of the weather station) on the lower slopes of Twin Peaks between 1740–1800 m. The site was sampled with ten 7 × 50 m rectangular quadrats. The Ajo Mountain site (32°00′N, 112°42′W) was located on the lower slopes of the Ajo Mountains from 2120–2200 m (within 2 km of the backcountry raingauge in the Ajo Mountains). This site was sampled with three 7 × 50 m quadrats. The area sampled was smaller for the Ajo Mountain site because there was less homogeneous habitat available for quadrat placement than in the Twin Peaks site. For all individuals within the sampling quadrats, the height of the tallest arm, the number of arms, and the presence or absence of buds, flowers, or fruits were recorded.

Fruit and seed samples. Nineteen ripe fruits were collected from *S. thurberi* plants within the two study sites. Each fruit was taken

TABLE 1. CLIMATIC SUMMARY AND CONDITIONS IN THE YEAR PRIOR TO STUDY IN ORGAN PIPE CACTUS NATIONAL MONUMENT. Means and standard deviations (s.d.) for the official station (near Twin Peaks) are calculated for the period 1951–1980 with data published by the Weather Bureau (1951–1974) and NOAA (1975–1980); mean and s.d. for freeze frequency are based on the 29 yr period excluding 1980 because of missing data. The previous year is defined as 1975 for annual and summer precipitation and as the winter of 1975–1976 for the number of freezes/winter. Mean and s.d. for the Ajo Mountains are based on data from a backcountry raingauge monitored by the Monument staff for the period 1962–1983 (exclusive of 1967 and 1973–1976).

	Official station			Ajo Mountains	
	$\bar{X} \pm$ s.d.	Range	Previous year	$\bar{X} \pm$ s.d.	Range
Annual precipitation (mm)	233 ± 78	87–377	111	342 ± 154	132 ± 657
Summer precipitation (mm) (June–September)	107 ± 56	17–192	17	—	—
Freezes/winter	19 ± 7	5–34	20	—	—

from a different individual. After removal of any persistent spines and dried flower parts, fruit lengths and maximum diameters were measured with a dial caliper graduated by 0.05 mm. Fruits were weighed with a triple beam balance immediately after collection. Seeds were then separated from the flesh of the fruits with a sieve. Seeds were air dried and weighed, and the number per fruit was determined. Seeds were stored for about 30 days in the dark at 20–25°C before they were used in germination tests.

Seed germinability was determined on a random sample (100 seeds) of those collected. These were placed in covered glass dishes on moist loam and sand combined in a 1:1 ratio. The dishes were kept at 20–25°C and exposed to 12 hr of fluorescent light/day (400 $\mu E \cdot m^{-2} \cdot s^{-1}$). Germination was monitored daily for five days.

RESULTS

Size and reproductive activity. Differences were apparent between the two study sites in the relationship of reproductive activity to size (Fig. 2, Table 2). The shortest individuals sampled that bore flowers or fruits were 0.99 m tall in the Twin Peaks site and 1.32 m tall in the Ajo Mountain site. In the Twin Peaks site, only three of 14 plants that flowered and were less than 1.49 m in height failed to produce fruits, whereas in the Ajo Mountain site, two of the four reproductively active individuals in the same size range failed to fruit. Despite the greater minimum height of reproductive activity in the Ajo Mountain site, the threshold height above which all plants

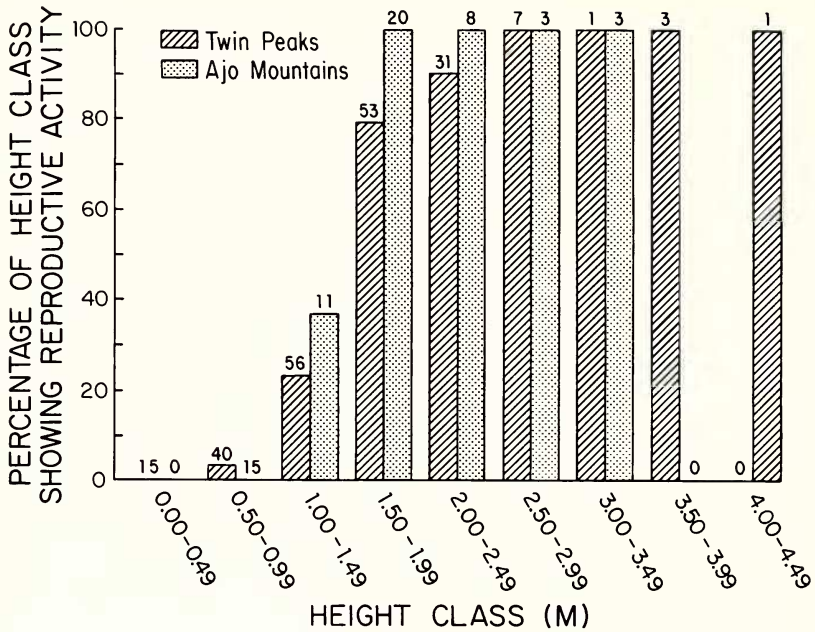

FIG. 2. The percentage of each height class showing evidence of reproductive activity of *Stenocereus thurberi* in the two study plots. Numbers above the bars indicate sample size for each height class.

in that sample produced flowers or fruits was lower (1.50 m) than in the Twin Peaks sample (2.50 m). Similarly, in the Ajo Mountain sample, all plants with more than seven arms produced flowers and fruits (Table 2) during the year of study, whereas in the Twin Peaks sample several plants with more than 10 arms did not flower. Three of the individuals in the Twin Peaks site greater than 2 m tall and with at least seven arms bore flowers, but not fruits. Despite these differences between the two samples, the overall relationship of size to reproductive activity suggests that most individuals of *S. thurberi* begin reproductive growth by the time they are 2–2.5 m tall. By this time, most plants have 4–10 arms.

Seed production per fruit and germinability. Fruits of *S. thurberi* are spherical in shape (Fig. 3, Table 3). The mean weight of the ripe fruits collected was 73.03 g. The significant intercorrelation ($p < 0.001$; Table 4) between fruit dimensions and weight indicates that these characteristics all vary proportionally. On average, seeds accounted for only 3.76 g of the total fruit weight. The mean number of seeds per fruit was 1969, and larger fruits generally produced more seeds than smaller fruits (Table 4). The mean seed weight per

TABLE 2. RELATIONSHIP OF REPRODUCTIVE STATUS TO ARM NUMBER IN *S. thurberi* AT TWO SITES IN ORGAN PIPE CACTUS NATIONAL MONUMENT. Reproducing plants include individuals bearing buds, flowers, or fruits. RP = the number of reproducing plants; n = the sample size for each arm-number category.

Number of arms	Twin Peaks (N = 207) Reproducing plants		Ajo Mountains (N = 60) Reproducing plants		Total (N = 267) Reproducing plants	
	RP/n	%	RP/n	%	RP/n	%
1	0/11	(0.0)	—	—	0/11	(0.0)
2	0/19	(0.0)	1/5	(20.0)	1/24	(4.2)
3	1/27	(3.7)	0/5	(0.0)	1/32	(3.1)
4	6/23	(26.1)	6/14	(42.9)	12/37	(32.4)
5	7/16	(43.7)	4/5	(80.0)	11/21	(52.4)
6	13/24	(54.2)	2/5	(40.0)	15/29	(51.7)
7	10/16	(62.5)	5/6	(83.3)	15/22	(68.2)
8	7/10	(70.0)	3/3	(100.0)	10/13	(76.9)
9	9/15	(60.0)	5/5	(100.0)	14/20	(70.0)
10	10/10	(100.0)	4/4	(100.0)	14/14	(100.0)
>10	33/36	(91.7)	8/8	(100.0)	41/44	(93.2)

fruit was not correlated significantly with any of the other fruit characteristics measured (Table 4). Eighty-eight percent of the *S. thurberi* seeds planted had germinated after five days.

DISCUSSION

Reproductive characteristics. In Saguaro National Monument, located approximately 150 km east of OPCNM, Steenbergh and Lowe (1977) reported a minimum reproductive height for *C. gigantea* similar to that reported here for *S. thurberi.* They found that all individuals greater than 2.5 m tall produced reproductive structures and that the smallest individual that showed evidence of reproductive activity was between 1.5 and 1.99 m tall. Steenbergh and Lowe (1977) concluded that healthy *C. gigantea* individuals typically reach reproductive maturity at a height of 2.2 m, or an age of about 30 yr.

Important differences exist between the two species in the relationship of arm number to reproductive activity. Steenbergh and Lowe (1977) found that individuals of *C. gigantea* begin to develop arms after they reach a height of approximately 4.5 m, or more than twice the size at which they typically begin reproducing. In southern Arizona, *S. thurberi* consists of many relatively narrow stems (ca. 15 cm diameter) that emerge from the base of the plant, rather than a primary stem with arms forming several meters above the base. Unlike *C. gigantea, S. thurberi* individuals generally do not begin reproducing until after they have more than one arm.

Steenbergh and Lowe (1977) hypothesized that the production of

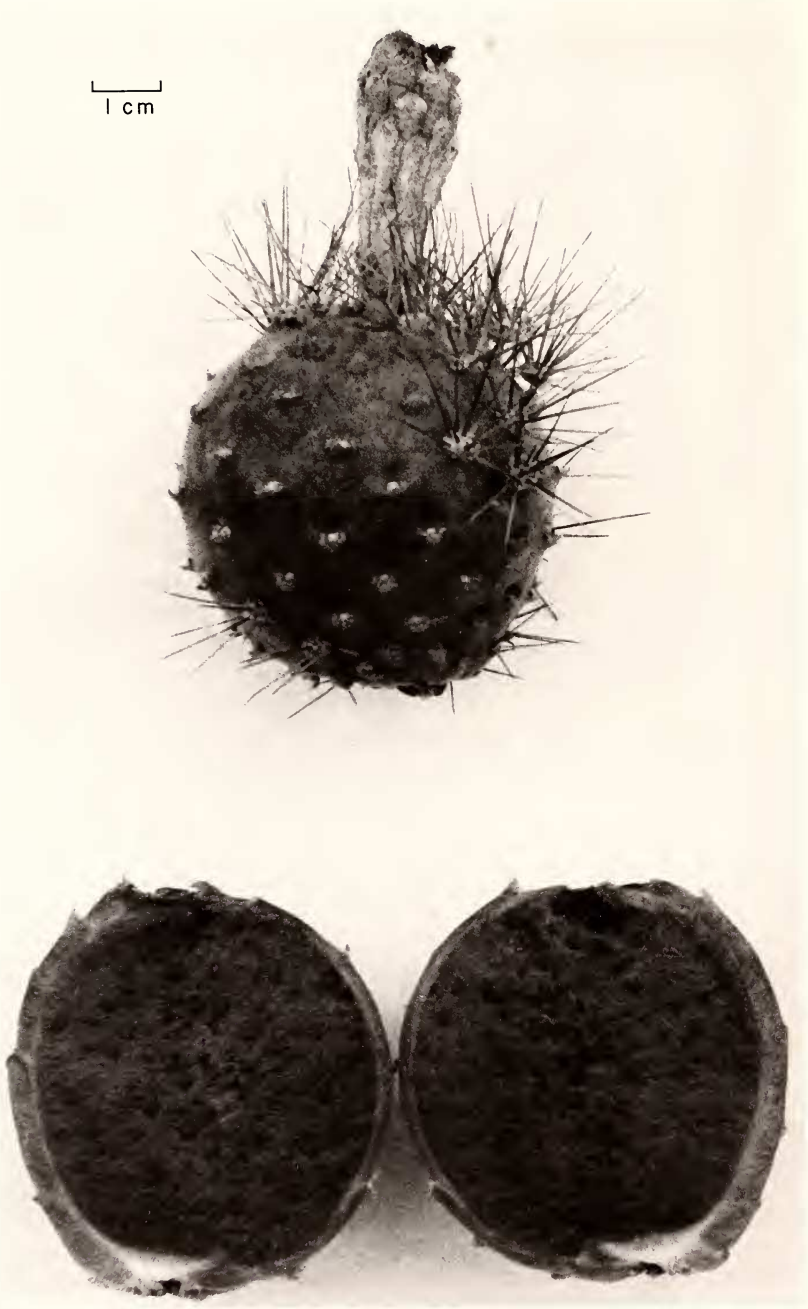

FIG. 3. Fruit of *Stenocereus thurberi.*

TABLE 3. DIMENSIONS, WEIGHT, AND SEED NUMBER OF FRUITS OF *Stenocereus thurberi* (n = 19). Whole fruits were measured with spines and desiccated flower parts removed; seeds from each fruit were air dried after removal of pericarp and flesh. The mean weight/seed by fruit for the sample was calculated by averaging the means for each fruit.

Measurement	$\bar{X} \pm$ s.d.	Range
Whole fruits		
Length (mm)	51.1 ± 6.5	41.4–63.3
Diameter (mm)	52.9 ± 4.9	41.7–63.5
Weight (g)	73.03 ± 23.18	32.19–125.22
Seeds per fruit		
Total weight (g)	3.76 ± 1.43	1.63–6.56
Total number	1969 ± 703	688–3373
Weight/seed by fruit (mg)	1.91 ± 0.23	1.47–2.37

arms in *C. gigantea* increases its reproductive potential and that this is their primary function. Undoubtedly, individuals of *S. thurberi* with numerous arms have a greater reproductive potential than those with few arms, because fruits are only borne on the upper portion of the arms. Whether enhancement of reproductive capacity serves as a selective force in arm production by *S. thurberi,* or is simply a fortuitous consequence of a basally-branched form conferred by different selective constraints is debatable.

Steenbergh and Lowe (1977) reported a slightly greater mean seed number per fruit for *C. gigantea* than I obtained for *S. thurberi,* although results of a t-test ($t = 1.51$, $df = 31$) indicate that this difference is not significant ($p < 0.05$; data for *C. gigantea* fruits were taken from Steenbergh and Lowe 1977). The mean seed weight for *S. thurberi* (1.9 mg) is greater than that reported by Steenbergh and Lowe (1977) for *C. gigantea* (1.3 mg), but the absence of a standard deviation value for mean seed weight for *C. gigantea* precluded calculation of the t-statistic to determine whether this difference is statistically significant.

TABLE 4. SPEARMAN CORRELATION COEFFICIENTS (r_s) BETWEEN FRUIT CHARACTERISTICS (n = 19). ** = significant at $p < 0.0001$; * = significant at $p < 0.05$.

	Mean weight/ seed	Seed number	Total seed weight	Fruit weight	Fruit diameter
Fruit length	0.04	0.45	0.39	0.86**	0.82**
Fruit diameter	−0.03	0.47*	0.42	0.95**	
Fruit weight	0.11	0.47*	0.42		
Total seed weight	0.10	0.94**			
Seed number	−0.10				

The germination percentage that I found for *S. thurberi* was similar to the 91% germination for this species (at 25°C with 8 hr photoperiods for 6 days) reported by McDonough (1964). Under the same conditions, he found a slightly higher percentage germination (97%) for *C. gigantea.*

Relationships between environment and reproductive activity. The mean number of fruits borne by individuals of *S. thurberi* was not quantified. Many plants observed during the course of data collection, however, bore at least 50 fruits. With a mean of approximately 2000 seeds per fruit, individuals that bear more than 50 fruits produce about 100,000 seeds in a single season. The results of the germination test indicate that a high percentage of the seeds produced by an individual have the potential of germinating if environmental conditions are favorable. Thus, the reproductive potential of even a small population of *S. thurberi* is great. Field germination percentages and the survival of seedlings, however, have not been determined.

In the Twin Peaks site, some large individuals of *S. thurberi* did not reproduce during 1976, and some that flowered failed to set fruit. Flowering and fruiting among large plants were more consistent in the Ajo Mountain site than in the Twin Peaks site. Variation in moisture regimes between the two study sites may be responsible, in part, for the differences in reproductive activity. In a particularly dry year, such as the one preceding the study, the higher rainfall characteristic of the Ajo Mountains may foster consistent reproductive activity of *S. thurberi* occurring there, while reproductive activity is more sporadic in drier parts of the Monument. Although Thackery and Leding (1929) and Steenbergh and Lowe (1977) reported that drought had little influence on fruit production in the closely related *C. gigantea,* Thackery and Leding (1929) suggested that reproductive activity in *S. thurberi* is more sensitive to drought stress than in *C. gigantea.* Steenbergh and Lowe (1977) also reported that severe freezes may reduce greatly the reproductive activity of *C. gigantea* the following summer. It is unlikely, however, that spatial variation in the occurrence of severe freezes caused the differences in reproductive activity between the two *S. thurberi* sites because of their similar topographic positions (i.e., susceptibility to cold air drainage).

The reproductive traits of *S. thurberi* are well adapted to the variable environment characteristic of the region of study. Near the margin of its range, successful establishment of young individuals of *S. thurberi* is limited by frequent severe freezes (Nobel 1980) and by periodic prolonged drought. Most individuals of *S. thurberi* become reproductively active at heights from 2–2.5 m. The fruiting of very large individuals indicates that plants are reproductively active

throughout most of their adult life. By producing a large quantity of seeds every year for many years, individuals of *S. thurberi* improve the chance that an occasional seed will disperse to a site favorable for germination and growth in a year when climatic factors are favorable, thereby maintaining a stable population.

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Literature Cited

Hastings, J. R., R. M. Turner, and D. K. Warren. 1972. An atlas of some plant distributions in the Sonoran Desert. Tech. Rep. on the Meteorology and Climatology of Arid Regions No. 21. Univ. of Arizona Institute of Atmospheric Physics, Tucson.

McDonough, W. T. 1964. Germination responses of *Carnegiea gigantea* and *Lemaireocereus thurberi*. Ecology 45:155–159.

National Oceanic and Atmospheric Administration. 1975–1980. Climatological data: Arizona. Vol. 79–84. U.S. Dept. Commerce, Washington, DC.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. Science 142:15–23.

Nobel, P. S. 1980. Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. Ecology 61:1–7.

Shreve, F. 1910. The rate of establishment of the giant cactus. Plant World 13: 235–240.

Smith, S. D., B. Didden-Zopfy, and P. S. Nobel. 1984. High-temperature responses of North American cacti. Ecology 65:643–651.

Steenbergh, W. F. and C. H. Lowe. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. Ecology 50:825–834.

——— and ———. 1977. Ecology of the saguaro: II reproduction, germination, establishment, growth, and survival of the young plant. Natl. Park Serv. Sci. Monogr. Ser. No. 8.

——— and ———. 1983. Ecology of the saguaro: III growth and demography. Natl. Park Serv. Sci. Monogr. Ser. No. 17.

Thackery, F. A. and A. R. Leding. 1929. The giant cactus of Arizona: the use of its fruits and other cactus fruits by the Indians. J. Hered. 20:400–414.

Weather Bureau. 1951–1974. Climatological data for the United States by sections: annual summary. Vols. 57–80. U.S. Dept. Commerce, Washington, DC.

Yeaton, R. I. and M. L. Cody. 1979. The distribution of cacti along environmental gradients in the Sonoran and Mojave deserts. J. Ecol. 67:529–541.

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